



DEPARTMENT OF AGRICULTURE AND FISHERIES
FOR SCOTLAND

Freshwater and Salmon Fisheries Research

36

Fertilization Experiments in Scottish Freshwater Lochs II.

Sutherland, 1954

2. Effects on the Bottom Fauna

By N. C. MORGAN, B.Sc.

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in Scottish Freshwater Lochs II.
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2. Effects on the Bottom Fauna**

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Fertilization Experiments in Scottish Freshwater Lochs II.

Sutherland, 1954

2. Effects on the Bottom Fauna

INTRODUCTION

Although many studies have been carried out on the effects of the addition of chemical fertilizers to artificial fish ponds and natural lakes most of these have only followed the chemical changes and the effects of these on the plankton or the fish stocks, and relatively few observations have been made on the bottom fauna organisms. Holden (1959) has described the chemical and botanical effects of the addition of mineral fertilizers to a series of relatively unproductive lochs with acid or neutral waters in west Sutherland. These lochs contain populations of brown trout (*Salmo trutta* L.) and the primary purpose of the experiments was to observe the effects of the addition of fertilizer on the growth rate of the trout (Munro, 1961). Since any increase in the growth rate of the trout was likely to operate through an increase in the bottom fauna or zooplankton populations the opportunity was taken of following the effects of the fertilization programme on the bottom fauna. The results of this study are presented here.

LOCHS SAMPLED

Quantitative assessments of the bottom fauna population were made in two of the lochs, Lochan an Smuraich and Loch Grosvenor, to which fertilizer was added. They are both situated on the north side of Loch Stack in north-west Sutherland in rugged, treeless country of low biological productivity. The underlying rock is Lewisian gneiss with a series of acid intrusions and this projects in many places through a covering of peat which supports a moorland vegetation of which heather, *Calluna vulgaris* (L.) Hull, is the artificial climax due to burning and grazing. On the wetter ground *Sphagnum* moss dominates and bog myrtle (*Myrica gale* L.) is prevalent. The lochs are 1.5 miles (2.4 km) apart.

TABLE 1

CHARACTERISTICS OF THE LOCHS STUDIED

Loch	Area		Mean depth		Max. depth		pH	Alkalinity
	(acres)	(ha)	(ft)	(m)	(ft)	(m)		
Lochan an Smuraich . . .	5.9	2.4	15	4.6	28	8.5	5.7	1.0
Loch Grosvenor	6.2	2.5	10	3.1	20	6.1	5.8	2.0

Table 1 shows some of the physical characteristics and the pH and alkalinity prior to fertilization. The spring and autumn water temperatures of the two lochs were always within 1°C of each other and, between 1954 and 1961, the mid-April water temperature ranged from 7.0–9.5°C and the late September to early October water temperature from 9.0–11.5°C. Lochan an Smuraich was 140 ft (43 m) and Loch Grosvenor 190 ft (58 m) above sea level.

The shoreline of Lochan an Smuraich varied from compacted sand to stones up to 1 ft (30 cm) across lying on or in compacted sand and gravel. Below the shoreline the bottom consisted of a thick soft brown mud which passed easily through a 40 mesh to one inch sieve leaving a fine debris much of which consisted of the broken remains of the exoskeletons of arthropods. In the sandier parts of the shoreline

TABLE 2

THE BOTTOM FAUNA OF THE LOCHS PRIOR TO FERTILIZATION										Lochan an Smuraich	Loch Grosvenor
ANNELIDA											
Oligochaeta										+	+
Naididae										++	++
Stylaria spp.										++	++
Lumbriculidae											
CRUSTACEA											
Cladocera											
Sida crystallina (Müll.)										+	+
Eurycerus lamellatus (Müll.)										++	++
INSECTA											
Plecoptera											
Isoperla grammatica (Poda)										-	+
Leuctra hippopus (Kempny)										+	+
Capnia bifrons (Newman)										+	-
Chloroperla torrentium (Pictet)										+	+
Nemoura cinerea (Retzius)										+	+
Ephemeroptera											
Caenis horaria (L.)										+	-
Ecdyonurus spp.										+	-
Leptophlebia marginata (L.)										++	++
L. vespertina (L.)										++	++
Cloeon simile Etn.										+	-
Odonata											
Pyrrhosoma nymphula (Sulz.)										+	-
Enallagma cyathigerum (Charp.)										-	+
Libellula quadrimaculata L.										+	+
Hemiptera											
Corixa scotti (D. & S.)										++	-
Velia spp.										+	+
Neuroptera											
Sialis lutaria L.										+	+
Trichoptera											
Phryganeidae										+	+
Limnophilidae										+	+
Lepidostomatinae										+	-
Leptoceridae										-	+
Mystacides azurea (L.)										+	+
Polycentropidae										++	+
Polycentropus flavomaculatus (Pict)										+	+
Cyrnus flavidus McLach.										++	-
Tinodes waeneri (L.)										-	+
Oxyethira spp.										+	++
Coleoptera											
Dytiscidae										+	+
Platambus spp.										+	+
Gyrinus spp.										-	+
Halplidae										+	-
Limnius tuberculatus Müll.										+	+
Latelmis volkmari Panzer										+	+
Diptera											
Pedicia spp.										-	+
Chaoborus spp.										+	-
Chironomidae										++	++
ARACHNIDA											
Hydracarina										++	+
MOLLUSCA											
Lamellibranchiata											
Sphaeriidae										+	+

- indicates not found

+ present, with a mean of less than ten animals per sample

++ present, with a mean of more than ten animals per sample

Littorella uniflora (L.) Aschers and *Lobelia dortmanna* L. were growing and in the deeper water *Nitella gracilis* Agardh, *Isoetes lacustris* L., *Eleogiton fluitans* (L.) Link and *Myriophyllum spicatum* L. were distributed over parts of the bottom.

The shoreline and mud at Loch Grosvenor were similar in physical characteristics to those of Lochan an Smuraich. The vegetation was not quite as rich and *Isoetes lacustris* and *Myriophyllum spicatum* were not found. The numerous arthropod remains in the mud of both lochs is unusual and is presumably due to very slow breakdown in the acid conditions. Although the mud fauna of many lochs in the Scottish Highlands has been examined arthropod remains in such quantities have not been noted elsewhere.

The bottom faunas (Table 2) were typical of those of the many low alkalinity acid lochs of the area. Plecoptera were common along the shoreline and *Leptophlebia marginata* (L.) and *L. vespertina* (L.) were by far the most abundant Ephemeroptera. Polycentropidae were the most common caddis larvae and the faunas of the mud were chiefly chironomid larvae. No Amphipoda were collected and the numbers of Oligochaeta were small. Mollusca were poorly represented.

FERTILIZATION PROGRAMME

The two lochs considered in the paper belonged to a series of four to which chemical fertilizers were added in 1954 and 1955 (Holden, 1959). Two lochs were treated with calcium superphosphate and two with NPK fertilizer to compare the effects of the two fertilizers on the growth of trout. One loch from each type of treatment was chosen for studies on the bottom fauna. These lochs were more acid than the other two and an initial application of ground limestone was added to raise the alkalinity. The treatments given are shown in Table 3.

TABLE 3

APPLICATIONS OF FERTILIZER

Lochan an Smuraich		
June 7	1954	10 cwt/acre ground limestone, 100 lb/acre 5:10:6 NPK fertilizer
August 3	1954	100 lb/acre 5:10:6 NPK
April 23	1955	6 cwt 4:10:7 NPK, 2 cwt sodium nitrate
June 15	1955	6 cwt 4:10:7 NPK, 2 cwt sodium nitrate
August 3	1955	6 cwt 4:10:7 NPK, 2 cwt sodium nitrate
Loch Grosvenor		
June 3	1954	10 cwt/acre ground limestone, 60 lb/acre calcium superphosphate
April 22	1955	3 cwt calcium superphosphate
June 15	1955	3 cwt calcium superphosphate
August 5	1955	3 cwt calcium superphosphate

In order to raise the nitrogen in the mixed fertilizer to the proportions 4N : 2P : 1K, as recommended by Swingle (1947), following his pond and glasshouse experiments on the requirements of phytoplankton, an extra amount was added in the form of sodium nitrate. The amounts of fertilizer added were calculated to add a total of approximately 25–30 lb of phosphorus per acre (28–33.5 kg/ha).

The fertilizers, which were in granular form, were applied from a boat and distributed as uniformly as possible over the whole loch. The ground limestone was applied from different points along the shore using an agricultural blower and resulted in uneven distribution with higher concentrations near the shore.

Although other lochs in the vicinity were used as chemical controls, various workers (Swingle, 1947; Ball, 1949; Patriarche and Ball, 1949) have found it impractical to obtain controls for the algal or bottom fauna communities. Swingle (1947) studied the production of planktonic algae in 27 quarter-acre ponds with a common water supply and practically identical in length, width and depth and found that 'when given identical fertilizer treatments, no two have the same appearance either to the naked eye or under the microscope'. It therefore seems unlikely that it would be possible to pick two lochs in the one area in which the bottom faunas were the same in all respects and, in any case, our present state of knowledge does not enable us to determine this. Therefore no other lochs were used in this study as controls for the bottom fauna.

METHODS

Quantitative samples of the bottom fauna of the mud of both lochs were taken using an Ekman grab (Ekman, 1911) similar in design to that described by Welch (1948). The original grab, used in 1954, sampled an area of 275 cm² and the closing flaps on the top were replaced by a copper gauze 40 meshes/inch (15.7 meshes/cm). This Ekman grab was unfortunately lost and the samples in the spring of 1955 were taken with an Ekman grab borrowed from the Freshwater Biological Association which sampled an area of 523 cm.² This was of conventional design with closing flaps on the top. From the spring of 1956 onwards the samples were taken using an Ekman grab sampling an area of 222 cm.² The closing flaps of this grab had been removed and a removable frame, covered with 40 mesh copper gauze (15.7 meshes/cm), fitted inside the grab at a height of 10 cm above the base when the jaws were open (Fig. 1).

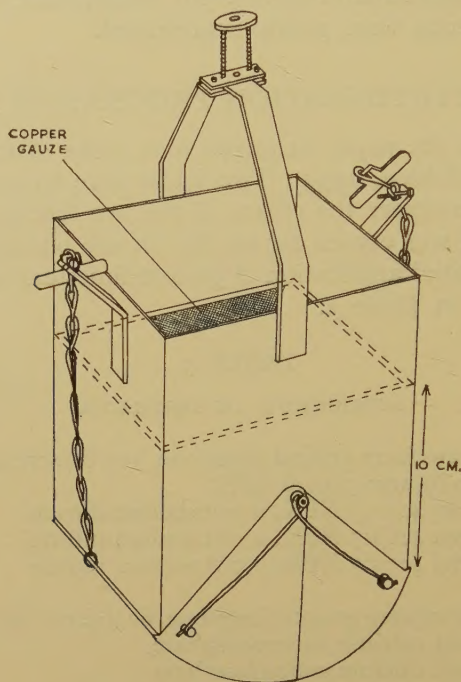


Fig. 1. Modified Ekman Grab.

This fitted tightly around the inside of the grab and was held in position by small brackets. The presence of the gauze prevented the grab from sinking more than 10 cm into the mud. The gauze frame could be removed and fitted to the open top of the grab so that the grab could sink its full depth of 17 cm into the mud. A comparison of the number and weight of animals caught by the grab from the same sampling station with the gauze set in the two different positions showed no significant difference. In other words there were no, or a negligible number of, animals of the size sampled by the grab in that region of the mud 10–17 cm below the surface and collection of a larger volume of mud, by allowing the grab to sink to its full depth, only increased the labour of sorting. It is to be noted in contrast that, in the much richer Esrom Lake, Berg (1938) found that a considerable number of animals occur down to about 30 cm and Lenz (1931) found animals down to 18–24 cm. Combining his results from eight lakes Berg found that 90% of the fauna occurred in the upper 15 cm of the mud and 75.5% in the upper 10 cm and further, that the major groups of animals present in the mud were all represented below 15 cm. These were, however, basically richer lakes than those considered in this study.

As animals, such as *Chaoborus* spp., common to both the bottom mud and water above the bottom were extremely uncommon in the lochs sampled, it was a distinct advantage to have a gauze top to the Ekman dredge. When the dredge was only fitted with hinged flaps on the top it was possible for it to

sink too far into the bottom with subsequent loss of animals in the richer upper zone of mud. Also there was a slight up and down movement of the flaps as the dredge was being drawn up to the water surface which again probably involved loss of animals. With the gauze set 10 cm above the base there was the added advantage that the upper 7 cm of the body of the dredge, above the gauze, was full of water when the dredge was lifted into the boat. If the jaws had not bitten properly into the mud this water drained away rapidly but if the dredge had functioned properly this water was retained. When the jaws of the dredge were opened to empty the contents the water drained through the gauze and washed out the inside of the dredge. This process washed the dredge so thoroughly that it was seldom found necessary to wash it out further.

One sampling site was chosen in each loch and four samples were taken at each site on each occasion. In a previous experiment in Loch Kinardochy, Perthshire, a total of 24 Ekman samples was taken, on the same date, from one site at a depth of 6 m. Statistical analysis of the results showed that the coefficient of variation of the mean of two samples was 15% for total numbers and 21% for total weights and of three samples the coefficients were 12% and 17% respectively. Also, for the commoner constituents of the fauna, e.g. *Gammarus lacustris*, Orthocladinae-Chironominae, Tanypodinae and *Pisidium* spp. the coefficient of variation of the mean of two samples was less than 40%. This degree of accuracy is sufficient to indicate the size of changes required if fertilization is to be a practical proposition. This experiment showed that three samples from one site were adequate in Loch Kinardochy but four samples were taken at each site in the present investigations because the biomass per unit area of the mud fauna was initially lower than in Loch Kinardochy (Table 10).

The sites chosen were at a depth of 5 m which was sufficiently deep to be below the influence of wave action. Samples were taken in the spring and autumn of each year from 1954 to 1959, with the exception of autumn 1955, and in the spring of 1960 and 1961. The spring samples were taken before most of the chironomid species had commenced to emerge and the autumn samples after the completion of the main emergence period (Morgan and Waddell, 1961). The bottom fauna could therefore be expected to be in a fairly stable state at these times and year to year comparisons to be valid.

The Ekman samples were sieved in the field through 40 mesh (wire thickness 0.2 mm, side of aperture 0.4 mm) sieves to remove excess mud, transferred to glass jars and transported immediately to a temporary laboratory. Here the animals were sorted from the organic debris while they were still alive using $\times 2$ magnification head magnifiers. 'Live' sorting was found greatly to facilitate the ease of this operation. Jónasson (1955) has shown that sieves with a mesh aperture of 0.20 and 0.26 mm retain very many more small chironomids than sieves of 0.51 and 0.60 mm mesh aperture. Thus a sieve of the size used above may be expected to lose many of the very small chironomid larvae. This loss was considered to be unimportant as the measurement of standing stock of bottom fauna animals was determined by weight of the total fauna as well as counts and the weight of the small animals lost was likely to be a very small fraction of the whole. Also if there was any increase in the number of a particular species following the addition of fertilizers this should show itself in the later instars which are retained by the sieve.

The animals from the samples were preserved in 70% alcohol and later counted, identified and weighed. The wet weight was determined by draining excess fluid off the animals and then drying their surface by rolling on a dry filter paper with a fine brush until they no longer dampened the filter paper. They were then weighed, by difference, in a stoppered weighing bottle on a balance accurate to 0.2 mg. The Sphaeriidae were weighed in their shells.

QUANTITATIVE CHANGES IN THE BOTTOM FAUNA

The changes in the total numbers and weight of animals caught per square metre of mud bottom at a depth of 5 m in Lochan an Smuraich and Loch Grosvenor from April 1954 to April 1961 are shown in Figs. 2 and 3. It would have been more desirable to have had a longer series of spring and autumn observations prior to fertilization in order to determine the natural fluctuations in numbers and weight of bottom fauna but this was not possible. Fortunately, the magnitude of the changes after fertilization was considerably greater than those normally occurring in lakes of this sort.

LOCHAN AN SMURAICH

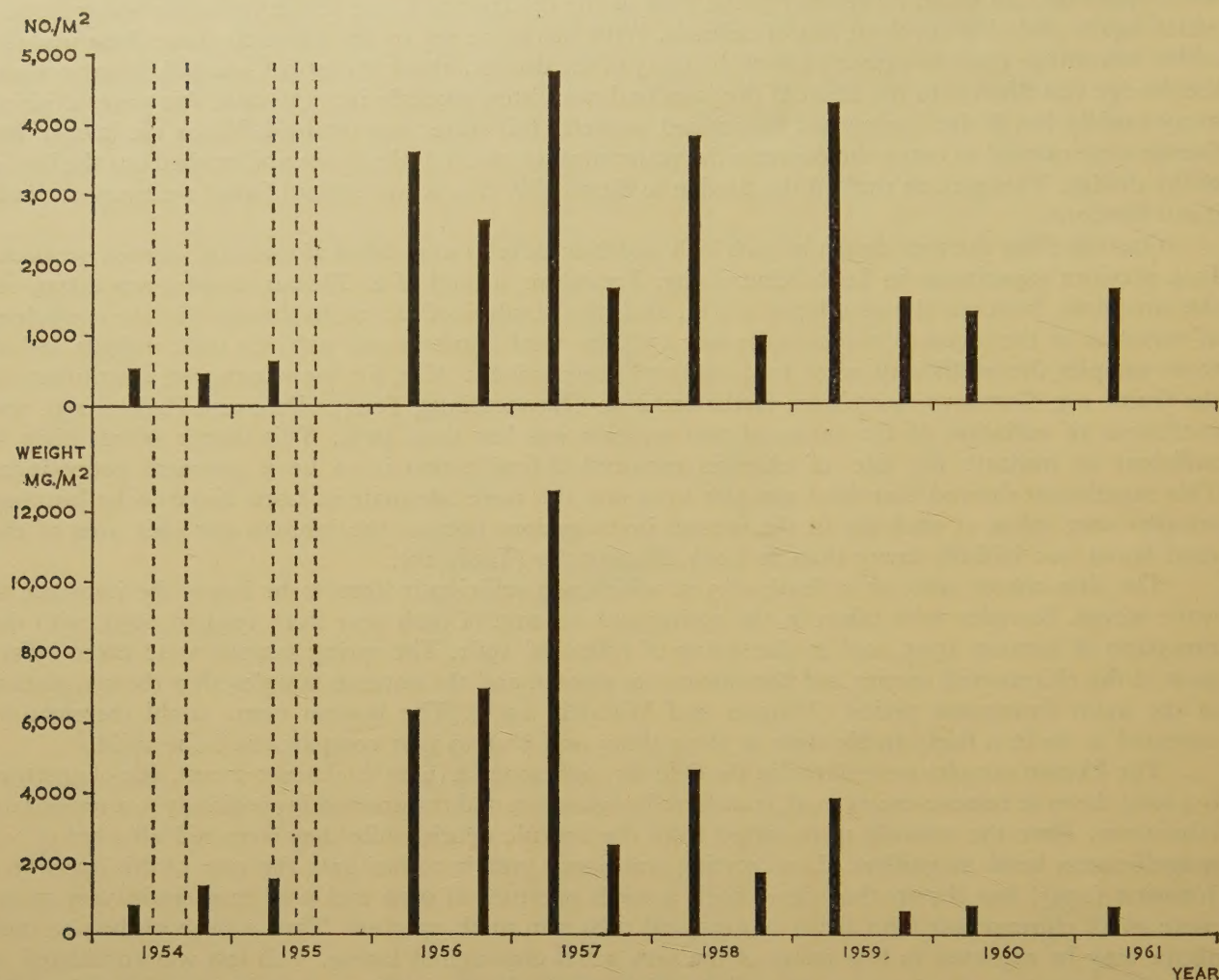


Fig. 2. Changes in the standing stock of the bottom fauna of the mud at 5 m. The verticle broken lines indicate the dates on which fertilizers were added.

In Lochan an Smuraich similar numbers of organisms were caught in the spring of 1954 and 1955 and the first apparent response to the addition of fertilizer was observed in 1956. The maximum was recorded in spring 1957, when there were nine times as many animals present as before fertilization. The numbers in the spring samples in 1958 and 1959 remained high, but were much lower in 1960 and 1961 although still two to three times the prefertilization level. The highest autumn density was recorded in 1956 and thereafter this declined, although at the last measurement in 1959, it was still three times the value in 1954. From 1957 onwards the autumn numbers and weights were considerably lower than in the spring of the same year.

A better measure of the effect of fertilization is given by the changes in total biomass of the bottom fauna. At Lochan an Smuraich the total weights were similar in 1954 and 1955 but by spring 1956 had increased to eight times the 1954 level. The build up continued in October 1956 to a striking maximum in April 1957 when the total weight of the standing stock of bottom fauna was sixteen times that in April 1954. After this the biomass declined until 1960 when it had returned to the prefertilization level.

The changes in density of animals showed a different pattern in Loch Grosvenor. The numbers rose to a peak in autumn 1956 and then declined to the autumn of 1957 when there were less than twice as many caught as in autumn 1954. After this there was an increase culminating in a maximum in April

LOCH GROSVENOR

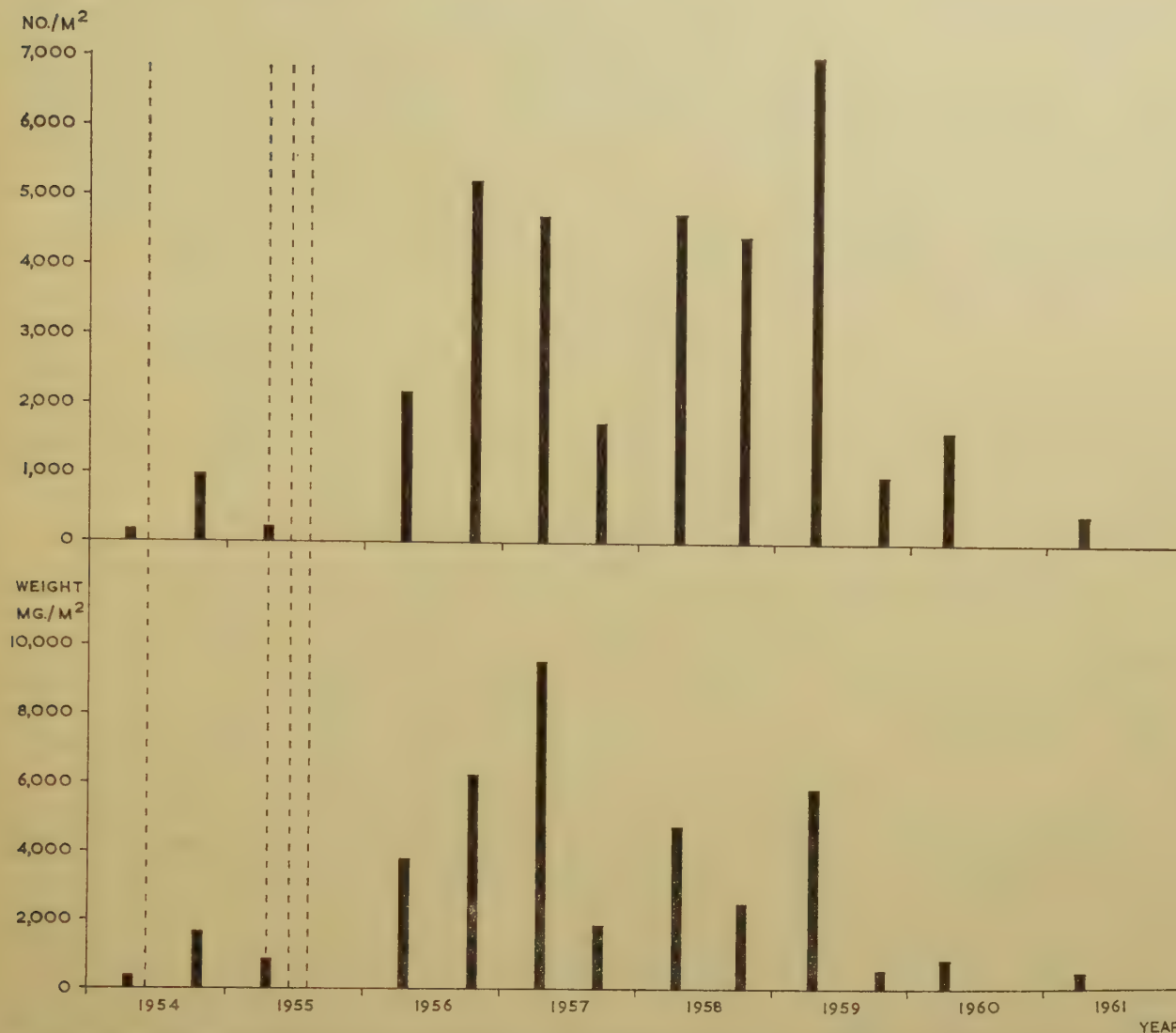


Fig. 3. Changes in the standing stock of the bottom fauna of the mud at 5 m. The verticle broken lines indicate the dates on which fertilizers were added.

1959 when 43 times the population in April 1954 was recorded. After this the total numbers declined rapidly and were of the same order as prior to fertilization by April 1961.

The changes in total biomass at Loch Grosvenor were similar to those observed at Lochan an Smuraich with the maximum occurring in April 1957, when the biomass was twenty-five times higher than that in April 1954. There was a slight secondary increase in the spring of 1959 corresponding to the maximum recorded population density but the weight of organisms had returned to the 1954 level by April 1960 and remained at this level in 1961.

It is noteworthy that the autumn numbers and weights at Loch Grosvenor in 1954 were higher than those in the spring, which is somewhat unusual, whereas at Lochan an Smuraich they were of the same order. This may have been the normal seasonal variation produced by the particular complex of species living in Loch Grosvenor or a more rapid response to the addition of fertilizer. The former is the more likely as the spring level in 1955 was again low. The decline in numbers and biomass between the spring and autumn samples from 1957 onwards at both lochs is due to the depletion of the fauna caused by the emergence of insects during the summer months. The autumn numbers are probably excessively low

since many early instar chironomid larvae, which would pass through the 40 mesh sieve (Jónasson, 1955), should then be present. However the total weight would be influenced little by this loss of minute larvae.

Unfortunately it was not possible to sample either loch in the autumn of 1955 but, from the higher spring figures in 1956, it can be deduced that the catches would probably have been higher than in 1954 since the larvae present in the spring of 1956 developed from eggs laid in the summer of 1955. It is therefore likely that the first detectable increase in bottom fauna occurred in the late summer or autumn of 1955 and this continued during 1956 when the increase in biomass was more rapid than the natural depletion during the summer months. The maximum production of bottom fauna, as shown by total biomass, did not occur until nearly two years after the last addition of fertilizer and three years after the first addition, and remained higher than the prefertilization level for another two years.

TABLE 4
NUMBERS OF LARGER AND SMALLER CHIRONOMIDAE (PER M²) IN LOCHAN AN SMURAICH IN SPRING

	Year							
	1954	1955	1956	1957	1958	1959	1960	1961
Larger Chironomidae	145 (35)	259 (48)	1655 (49)	2016 (44)	1126 (31)	1076 (26)	166 (14)	391 (28)
Smaller Chironomidae	273 (65)	278 (52)	1746 (51)	2544 (56)	2456 (69)	3017 (74)	1018 (86)	1030 (72)
Total	418	537	3401	4560	3582	4093	1184	1421

Figures in brackets indicate the percentage of the total Chironomidae

TABLE 5
NUMBERS OF LARGER AND SMALLER CHIRONOMIDAE (PER M²) IN LOCH GROSVENOR IN SPRING

	Year							
	1954	1955	1956	1957	1958	1959	1960	1961
Larger Chironomidae	127 (88)	109 (92)	1216 (61)	1745 (43)	992 (26)	1229 (20)	426 (30)	130 (61)
Smaller Chironomidae	18 (12)	9 (8)	766 (39)	2297 (57)	2782 (74)	4989 (80)	1005 (70)	83 (39)
Total	145	118	1982	4042	3774	6218	1431	213

Figures in brackets indicate the percentage of the total Chironomidae

The bulk of the response to fertilizer was produced by an enormous increase in the number of chironomid larvae which were the predominant group in the mud fauna prior to fertilization. At their maxima the catches of chironomids at Lochan an Smuraich were eleven times and at Loch Grosvenor 43 times the numbers present before fertilization. The other animals showed no, or only slight, increases in the numbers caught. As the numbers of organisms remained high in the springs of 1958 and 1959, when the total weight was decreasing, the mean size of animals present must have decreased. This is related to a change in the proportions of different species of Chironomidae present and is illustrated in Tables 4 and 5. Here the Chironomidae have been divided into two groups based on the size of the last instar larvae which in the 'larger Chironomidae' is over 5 mm and in the 'smaller Chironomidae' 5 mm or less. The larger Chironomidae consisted chiefly of *Ablabesmyia* spp., *Procladius* spp., *Microtendipes chloris* Meig. and *Polypedilum* spp. and the smaller Chironomidae of *Orthocladus apicalis* Kief., *Lauterborniella orophilus* Edw. and *Tanytarsus* spp. In Table 6 the weights of these groups are compared, based on measurements made on adult chironomids from Loch Dunmore, Perthshire. The biomass of the smaller species is three to thirteen times lower than that of the larger species.

TABLE 6
FRESH WEIGHTS OF ADULT CHIRONOMIDAE

	Weight (mg)	
	Males	Females
Smaller species		
Lauterborniella orophilus Edw.	0.3	0.3
Tanytarsus spp. (mean of 9 spp.)	0.3	0.4
Larger species		
Ablabesmyia spp. (mean of 6 spp.)	1.0	1.4
Procladius spp. (mean of 3 spp.)	2.2	3.1
Microtendipes chloris Meig.	1.4	2.6
M. chloris var lugubris Kieff.	2.4	4.1
Polypedilum spp. (mean of 3 spp.)	0.6	1.2

In Lochan an Smuraich the proportion of smaller to larger Chironomidae was approximately 2:1 prior to fertilization. There was a slight increase in the proportion of larger species in the following year and from 1955 to 1957 the number of large and small increased in proportion to one another. From 1957 onwards the proportion and number of larger larvae fell to a minimum in 1960 whilst at the same time the number of smaller larvae increased slightly. Hence the steady decline in total weight of samples between 1957 and 1959, in spite of the relatively stable total numbers. By 1961 the two groups were showing a trend towards the prefertilization proportions.

In contrast to Lochan an Smuraich the proportion of larger Chironomidae at Loch Grosvenor was much higher than that of the smaller species before fertilization. From 1955 onwards there was an increase in the numbers and proportion of smaller species to a maximum in 1959 when they formed four-fifths of the chironomid fauna. In spite of the extremely large numbers of Chironomidae present in 1959 the total weight of animals was considerably higher in spring 1957 when there were more larvae belonging to larger species present. The proportion of smaller species declined in 1960 and 1961, showing a trend towards prefertilization conditions.

Although the overall changes in total weight were similar at both lochs following the addition of fertilizer, the changes in the composition of the fauna were somewhat different and different species predominated in the fauna from year to year. The addition of fertilizer may have upset the trophic conditions existing within the lochs and produced unstable conditions under which the natural fluctuations in different species could be accentuated. This is particularly noticeable in Lochan an Smuraich (Appendix 1) where the predominant taxa each April were: *Lauterborniella orophilus* and *Procladius* spp. in 1954 and 1955, *Orthocladius apicalis* in 1956, *Tanytarsus* spp. and 'Other Chironomidae' in 1957, *Orthocladius apicalis* in 1958, *Tanytarsus* spp. and *Lauterborniella orophilus* in 1959, *L. orophilus* in 1960 and *L. orophilus* and *Tanytarsus* spp. in 1961. The autumn fauna was less variable with *Procladius* spp. predominating in three years out of five. In Loch Grosvenor *Tanytarsus* spp. were predominant from October 1956 to April 1960 with the exception of the autumn of 1957 (Appendix 2). It is interesting that, in both lochs, there was a rapid increase in the numbers of *Ablabesmyia* spp., the maxima occurring in April 1956, after which the numbers gradually declined. Thus maxima for different species occurred one, two, three and four years after the last addition of fertilizer. Although *Tanytarsus* spp. predominated in Loch Grosvenor following fertilization they were initially less abundant than at Lochan an Smuraich the numbers being so low that they were not detected in the springs of 1954 and 1955. They were, however, present in the autumn of 1954 whereas at Lochan an Smuraich they were more abundant in the spring than in the autumn prior to fertilization.

The tendency for large numbers to be caught in the autumn continued after fertilization in Loch Grosvenor. This may indicate the presence of different species of *Tanytarsus* in the two lochs, those at Loch Grosvenor being more capable of exploiting the conditions brought about by the addition of inorganic fertilizer. The changes in numbers of *Tanytarsus* illustrate the magnitude of the fluctuations which can take place. In Loch Grosvenor the number per square metre rose from 18 in October 1954 to 2286 in October 1956, declined to 360 in September 1957, rose to 4434 in April 1959 and fell to 12 by April 1961. It is difficult to discern why such a prominent maximum should occur four years after the last addition of fertilizer, though similar maxima for *Lauterborniella orophilus* and *Tanytarsus* spp. were recorded at this time at Lochan an Smuraich. Phosphates are readily taken up by the phytoplankton and on the mud surface (Holden, 1961). Caines (1965) has shown that the proportion of total phosphorus in aquatic macrophytes increases following the application of NPK and superphosphate fertilizers to the environment and, in experiments with the addition of fertilizers to fish ponds, Swingle (1947) found that sometimes, when the phytoplankton algae died, almost all the nutrients released went into the production of other algae, whereas in other instances they went into the production of animal organisms. The late maxima for some of the smaller chironomids may have been due to the release of phosphates from reservoirs such as these or, on the other hand, these species may have been dependent on the sequence of species which flourished before them.

The size and composition of the fauna in April 1961 suggest that six years after the last application of fertilizer the mud fauna had not quite returned to the prefertilization condition in both lochs.

TABLE 7

NUMBERS OF LARVAE OF TANYPODINAE, ORTHOCLADIINAE AND CHIRONOMINAE (PER M³) IN LOCHAN AN SMURAICH, 1954-61

	Tanypodinae		Orthoclaadiinae and Chironominae		Ratio a : b
	(a)		(b)		
Apr. 1954 . .	118		300		1:2.5
Oct. 1954 . .		245		64	1:0.26
Apr. 1955 . .	211		326		1:1.5
Apr. 1956 . .	1193		2208		1:1.8
Oct. 1956 . .		821		1709	1:2.1
Apr. 1957 . .	991		3569		1:3.6
Sept. 1957 . .		777		618	1:0.79
Apr. 1958 . .	1036		2546		1:2.5
Oct. 1958 . .		579		296	1:0.51
Apr. 1959 . .	946		3147		1:3.3
Oct. 1959 . .		177		1219	1:6.9
Apr. 1960 . .	142		1042		1:7.3
Apr. 1961 . .	237		1184		1:5.0

TABLE 8

NUMBERS OF TANYPODINAE LARVAE AND ORTHOCLADIINAE AND CHIRONOMINAE (PER M²) IN LOCH GROSVENOR 1954-61

	Tanypodinae		Orthoclaadiinae and Chironominae		Ratio a:b
	(a)		(b)		
Apr. 1954 . .	91		54		1:0.59
Oct. 1954 . .		218		381	1:1.75
Apr. 1955 . .	91		27		1:0.29
Apr. 1956 . .	597		1385		1:2.3
Oct. 1956 . .		743		4211	1:5.7
Apr. 1957 . .	1036		3006		1:2.9
Sept. 1957 . .		236		980	1:4.1
Apr. 1958 . .	496		3278		1:6.6
Oct. 1958 . .		438		3702	1:8.5
Apr. 1959 . .	414		5804		1:14.0
Oct. 1959 . .		118		545	1:4.6
Apr. 1960 . .	248		1183		1:4.8
Apr. 1961 . .	95		118		1:1.2

In the absence of many small Oligochaeta the carnivorous larvae of the Tanypodinae were almost entirely dependent on other chironomid larvae for food. The catches of Tanypodinae are compared with those of the larvae of Orthoclaadiinae and Chironominae in Tables 7 and 8. It might have been expected that the numbers of Tanypodinae would vary in proportion to the herbivorous Chironomidae and whereas, until autumn 1959, this was to some extent true at Lochan an Smuraich, they did not increase as expected at Loch Grosvenor. The Orthoclaadiinae and Chironominae increased at a greater rate than the Tanypodinae until, in the spring of 1959, they had increased 100 times since 1954 whereas the numbers of Tanypodinae were only four times those in 1954. By 1961 the proportion between the two groups was again about that in 1954. The failure of the Tanypodinae to increase further may have been due to predation by other invertebrates or fish or because the total biomass of animals could not support any larger number even though the numbers of smaller chironomid larvae were increasing. Indeed the total numbers of Tanypodinae in Loch Grosvenor rose and fell, from year to year, in phase with the rise and fall in the total biomass of bottom fauna organisms although not in proportion to it. Cannibalism by larger larvae on the earlier instars may also to some extent have been a self-limiting factor. Howell (1942) comparing the bottom fauna of an unfertilized and a fertilized fishpond, found that in the middle of summer over half the Chironomidae in the unfertilized pond were Tanypodinae whereas no Tanypodinae were caught in the fertilized pond.

The other members of the mud fauna did not respond to the addition of fertilizer as strikingly as the Chironomidae (Appendices 1 and 2). In Lochan an Smuraich there was no significant change in the numbers of Oligochaeta but in Loch Grosvenor the numbers increased. The Sphaeriidae probably increased in both lochs. Higher numbers were recorded in Loch Grosvenor in the springs of 1957, 1958 and 1959 than in the other spring samples although considerable numbers were caught in the autumn of 1954.

QUALITATIVE CHANGES IN THE BOTTOM FAUNA

During the period of the investigation handnet collections were taken at four shoreline stations and dredgings through two weed beds in deeper water at Lochan an Smuraich. At Loch Grosvenor handnet collections were taken at three shoreline stations and dredgings through three weed beds. The methods of sampling cannot be regarded as accurate ways of assessing the numbers of animals present but were intended to observe any changes in the species composition which might have taken place. The composition of the fauna in 1954 is shown in Table 2.

At Lochan an Smuraich no clear changes were detected in the composition of the shoreline and weed fauna following fertilization although *Cloeon simile* Etn., which was only found in one sample in the autumn of 1954, was more widespread and plentiful from 1955 to 1957.

At Loch Grosvenor *Cloeon simile* was only found in collections between 1955 and 1957, the largest catch being 17 in one dredging in 1957; *Limnaea peregra* (Müll.), which was not found in any samples in 1954, was found regularly from 1955 onwards. The handnet collections at one station where the bottom consisted of flat stones, up to 8 in. across, lying on compacted gravel with some *Lobelia dortmanna*, are shown in Table 9. A larger number of snails were caught here than elsewhere in the loch and it will be seen that the maximum number was caught in 1955 and 1956 after which the numbers declined. No changes were detectable in the composition of the rest of shoreline and weed fauna.

TABLE 9

THE NUMBERS OF *Limnaea peregra* CAUGHT AT ONE SHORELINE STATION IN LOCH GROSVENOR IN APRIL

Year	Number
1954	0
1955	32
1956	30
1957	9
1958	8
1959	0
1960	3

It is possible that *Limnaea peregra* invaded the loch from the outflowing burn following the addition of fertilizer and limestone as this snail was observed in the outflow burn in March, 1955 (Munro, personal communication). In 1955 an extensive development of the attached algal flora was observed between June and August (Holden, 1959). This would favour the development of *L. peregra*, which browses on these algae. At Loch an Daimh Mor, another loch to which superphosphate was added in 1954 and 1955 (Holden, *loc. cit.*), very large numbers of *L. peregra* were caught in handnet collections in 1956 and 1957 compared with earlier collections. This loch had an initial alkalinity of 11.8 mg CaCO₃/l and *L. peregra*, which was common in collections prior to fertilization, was able to exploit the extensive development of attached algae which occurred in this loch in 1955 and 1956. On the other hand a rich planktonic flora was produced in the lochs to which NPK fertilizer was added.

COMPARISON WITH THE BOTTOM FAUNA OF OTHER LOCHS

Table 10 shows the standing stock of the bottom fauna of a series of Scottish lochs ranging from very low productivity, dystrophic to high productivity, eutrophic conditions. The measurements are based on Ekman grab samples taken from mud during the winter or early spring at a depth of 5 metres

TABLE 10
THE BIOMASS OF BOTTOM FAUNA OF THE MUD OF SEVERAL
SCOTTISH LOCHS IN RELATION TO pH AND ALKALINITY

Loch	pH	Alkalinity (mg CaCO ₃ /l)	Weight of Standing Stock (g/m ²)
Loch Borrallie . . .	8.4	109	20.2
Loch Moraig . . .	7.8-8.2	50-70	20.8
Loch Leven . . .	7.7	51	36.8
Flemington Loch . . .	7.6	36	39.9
Loch of Marlee . . .	7.5	32	11.8
Loch Kinardochy . . .	7.2-7.6	15-25	5.12
Loch Faskally . . .	6.5-7.1	5-14	2.18
Loch Cruinn . . .	6.8-6.9	5-6	8.14 ^a
Loch Choin . . .	6.7-7.0	4-6	2.76
Loch Laga . . .	6.5	3.2	2.04
Loch Rannoch (Carie Bay)	6.6	3	0.36
Loch Grosvenor . . .	5.8	2	0.52
Lochan an Smuraich . . .	5.7	1	1.05

^a Slaked lime added, $\frac{1}{2}$ ton/acre 15.10.52. Sampled 9.12.53

or at the maximum depth of the loch if this was less. Previous work (unpublished) has shown that the alkalinity of a loch can be used as a guide to the productive level of the bottom fauna of the mud and the lochs shown in the table are arranged in order of descending alkalinity. It will be seen that, in general, the weight of bottom fauna per square metre increases with increasing alkalinity. The weight of bottom fauna present in Loch Moraig and Loch Borrallie is less than would be expected from their alkalinity values. The reason for this may be that, in limestone lochs, some of the excess calcium combines with free phosphate and makes the latter unavailable to the flora. On the basis of prefertilization measurements Lochan an Smuraich and Loch Grosvenor are at the lower end of the table. The maximum weight of the mud fauna reached in April 1957 was 9.5 g/m² at Loch Grosvenor and 12.6 g/m² at Lochan an Smuraich. Based on the table this is equivalent to the standing stock of bottom fauna in a loch with an alkalinity of about 30 mg CaCO₃/l. Lochs of this trophic level are capable of supporting a good trout fishery and therefore, on the basis of standing stock of bottom fauna, fertilization raised the productivity of two poor acid lochs to a satisfactory level.

DISCUSSION

Where bottom fauna studies have been carried out following the addition of inorganic fertilizers to lakes and fishponds, the observed increases in production have not been of the magnitude of those in the two base deficient Highland lochs studied here. Weatherley and Nicholls (1955) were not able to detect any change, Patriarche and Ball (1949) showed increases of 16 and 136%, Ball (1949) increases of 21 and 68%, Smith (1961) increases of just over two times and Howell (1942) increases of three and a half times. Rayment (1949) studying a sea loch on the west coast of Scotland recorded an increase of up to seven times in weight of bottom fauna. However, as in some of these studies observations were only made during the year when fertilizers were added, the full increase in the bottom fauna may not have been recorded. Smith (1961) found the bottom fauna increased to high levels two and three years after fertilization and that the levels declined to near prefertilization levels by the fourth and fifth years. In two sea lochs Rayment (1949, 1950) found that, with repeated applications of fertilizer, at least two to three years were necessary to achieve maximum production from the bottom fauna and in one loch the bottom fauna production was still more than twice as great as under natural conditions two years after regular fertilization was discontinued. These periods are similar to those observed in the studies recorded here. Since most of the bottom fauna organisms have a life cycle of one year or less it might be expected that the maximum production would occur sooner than this after the addition of fertilizer. This suggests that the right kind of food for bottom fauna does not increase immediately. The delay may be related to the time taken for the movement of the fertilizers through various components of the

ecosystem. For instance the phosphate could be adsorbed on to deposits such as the iron-organic-bacterial complexes or recycled through several generations of phytoplankton before being released to enrich the attached algae and macrophytes.

Chemical and botanical observations were carried out from 1954 to 1957 (Holden, 1959). During the two years following fertilization the organic phosphorus concentrations were significantly higher in Lochan an Smuraich and Loch Grosvenor than in two other lochs used as chemical controls, and were comparable with those found in lochs of higher productivity in Scotland. Although the effects of the fertilizer on the bottom fauna were evident for five or six years after the last fertilization, the total weight of mud fauna fell by a half in one loch and by nearly two-thirds in the other in the year following the maximum production. This indicates that it may be necessary to apply fertilizer annually if the maximum production of bottom fauna is to be maintained.

Holden (1959) has considered the economics of the experiments, of which Lochan an Smuraich and Loch Grosvenor were a part, based on the chemical and botanical findings. The evidence showed that phosphorus is an important, if not the principal, nutrient which is lacking and that the difference in the effect of calcium superphosphate and NPK fertilizers did not justify the high expense of the latter. The bottom fauna investigations support this conclusion as the biomass increased 25 times at Loch Grosvenor (superphosphate) compared with 16 times at Lochan an Smuraich (NPK). The use of NPK fertilizer might, however, be justified if this fertilizer brought about qualitative changes which were more beneficial for the trout population. Observations on the growth rate of the trout were recorded by Munro (1961) but as no measurements of the total biomass were made it is not possible to determine this point. However, Munro states that, although no attempt was made to make accurate estimates of the trout populations, there was no indication of changes in their density. If it is assumed that the population remained steady, then the total weight of fish in Loch Grosvenor in 1957 was about half as much again as in 1954 and in Lochan an Smuraich it was nearly double. The biomass of the bottom fauna, however, increased 25 and 16 times, which suggests that much of this increase was not utilised by the trout.

Up to 1957 the growth rate of trout at Lochan an Smuraich was higher than in 1953 but at Loch Grosvenor, although there was an immediate response to fertilization by increased growth rate in 1954, the calculated lengths of the younger fish had returned towards the prefertilization level in 1956 and 1957. The growth rate of fish increased prior to the recorded increase in bottom fauna, perhaps because they had fed on the large quantity of zooplankton which was produced in 1954. If the fish had been able to utilise the increasing numbers of bottom fauna organisms they would have been expected to maintain an increased growth rate in 1956 and 1957 and, until about 1959, their growth rate should have been higher than before fertilization (see Figs. 2 and 3).

It may well be that the addition of fertilizer to these lochs promoted an increase in the wrong type of bottom fauna organism to produce large trout. The increase was chiefly in chironomids and these are normally an important constituent of trout food in the spring and early summer (Allen, 1938; Frost and Smyly, 1952; Campbell, 1955; Nilsson, 1955). The chironomids are most available to trout during the short period of their life when they leave the cover of the bottom as active pupae prior to emergence, although Mundie (1959) has found larvae in the surface waters of Lac La Ronge at night and in mid-water at Esthwaite Water during the spring and summer (Freshwater Biological Association, Thirty-second Annual Report, pp. 30–31 (1964)). However, fish feeding studies confirm that more chironomid pupae than larvae are eaten by trout. At Loch Grosvenor and Lochan an Smuraich the smaller chironomid species showed the maximum response by numbers to fertilization, particularly *Orthocladus apicalis*, *Lauterborniella orophilus* and *Tanytarsus* spp. Although these smaller larvae are suitable for smaller trout, bigger fish require larger organisms to maintain a good growth rate, particularly during the period November to March when there is no emergence of adult insects. This is provided in rich lochs by the larger caddis larvae and permanent members of the bottom fauna such as *Gammarus* spp., *Asellus* spp. and aquatic snails. In the lochs to which fertilizer was added the fauna initially contained few species which provide good winter feeding for trout. The species of bottom fauna which increased following fertilization provided a rich seasonal abundance of food but the fish which responded to this by increased growth rate may thus have increased the competition amongst themselves for the unchanged food supply at other times of the year. If fertilization is to be successful, it is essential that the food supply at all times

of year should be increased as the production of fish will be limited by the food which is in the lowest seasonal supply. In future experiments with lochs of this type it would be advisable to compare the addition of fertilizer alone with the addition of fertilizer plus the introduction of new species to provide food suitable to maintain larger trout. It may well be that the growth rate of trout in many acid Highland lochs is poor not only because the standing stock of bottom fauna organisms is low, but because the wrong species of food organisms are present. Forms such as *Gammarus pulex* (L.), *Gammarus lacustris* Sars, *Asellus aquaticus* L., *Asellus meridianus* Racovitza and *Limnaea peregra* (Müll.), which are easily collected in large numbers and transport readily, would be suitable species for introduction. The author successfully established a breeding population of *Asellus aquaticus* in a new impoundment of about 16 acres by the introduction of 1000 adults. Conditions in a loch enriched by fertilizer may be similar in some respects to those in a newly formed loch since competition between species may be reduced giving new species a better chance of establishing themselves.

In many experiments with the addition of artificial fertilizers to warm water lakes the aim has been to produce a dense phytoplankton bloom with a resulting high production of zooplankton. This provides suitable food for some of the fish present in these waters but its value in trout waters is more doubtful. Phytoplankton blooms are easily produced by the addition of soluble inorganic fertilizers which become distributed throughout the water mass where they are available to the planktonic algae, which readily take them up. Although the nutrients which are locked up in this way may eventually become available to bottom-dwelling invertebrates, which are the staple food of trout, this probably leads to a delay in bottom fauna production, as instanced in this experiment, and is essentially wasteful. It would be better to try to stimulate the growth of the algae of the mud and the attached and epiphytic algae, which form a part or the whole of the diet of many members of the bottom fauna. This might be achieved by the use of a pelleted fertilizer, formulated so that the phosphate is released more slowly than from those used in this experiment, or by the use of organic fertilizers. Swingle (1947) found that organic fertilizers tended to produce filamentous algae, because they decayed slowly on the bottom, whereas inorganic fertilizers encouraged the growth of planktonic algae. Following the application of bone meal and limestone chips to a small tarn in April, Macan (1949) found that the bottom fauna of the mud increased numerically about ten times by March of the following year and, since fertilization, *Nitella* has spread to the deeper parts of the tarn where the mud was originally bare. Surber (1945) compared the effect of different organic and inorganic fertilizers on the production of smallmouth bass, in ponds, and found that Timothy hay plus superphosphate produced the biggest weight of fish compared with sheep manure, cotton seed meal, soya bean meal and NPK fertilizer used singly or in combinations of organic and inorganic fertilizers. Wlodek (1957) found that green manuring of fingerling ponds by flooding belts of growing rye increased the production of bottom fauna, mainly chironomids, about ten times but that barnyard manure had little effect. The culms or draft from whisky distilleries might prove to be a useful organic fertilizer which is locally available in Highland areas of Scotland. In the south-eastern United States of America, Smith and Swingle (1942) found that filamentous algae develop in winter or spring so that fertilizers should be added in the winter if their growth is to be promoted. Later application promotes phytoplankton blooms. Although Scotland is at a higher latitude and the life cycles of the algae are likely to be different, the effects of application of fertilizers in the winter time should be investigated. Also the direct effect of fertilizers on the growth of macrophytes (Caines, 1965) is an important link as many invertebrates such as *Gammarus lacustris*, *G. pulex*, *Limnaea peregra*, many of the larger caddis larvae and the plant-eating chironomids browse on the tissues of these plants.

This study has shown that the addition of inorganic fertilizers can bring about large increases in the bottom fauna of poor Highland lochs. Future work should be directed towards determining the best means of producing a bottom fauna which can be utilised efficiently as trout food, so that it is essential to know more about the stages between the addition of fertilizer and cropping the fish. The addition of fertilizer raised the biomass of bottom fauna in the mud to one quarter to one third of that of Loch Leven which supports a world famous trout fishery. It is still to be determined whether the addition of larger amounts of fertilizer or more frequent additions could attain a productivity equivalent to that of Loch Leven, under Highland conditions.

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SUMMARY

1. Quantitative samples of the bottom fauna of the mud were taken from two lochs, of 5.9 and 6.2 acres (2.4 and 2.5 ha) in area, in north-west Sutherland, to which inorganic fertilizers were added.
2. Calcium superphosphate was added to Loch Grosvenor and a mixed nitrogen-phosphorus-potassium fertilizer to Lochan an Smuraich. Several applications of fertilizer were made during the summers of 1954 and 1955.
3. There was no change in the biomass of bottom fauna in 1954 and 1955 but an increase occurred in both lochs in 1956, reaching a maximum in April 1957, when 25 times the April 1954 biomass was recorded at Loch Grosvenor and 16 times at Lochan an Smuraich. The total weight fell about one half to a third of this level in April 1958 and 1959 and returned to the prefertilization level in 1960 and 1961.
4. The total number of organisms also reached a maximum in April 1957 in Lochan an Smuraich (9 times the number in April 1954) but did not reach a maximum until April 1959 at Loch Grosvenor (43 times the catch in April 1954).
5. Most of the response to fertilizer was produced by a big increase in the number of chironomid larvae. In particular there was an increase in the number and proportion of larvae of the smaller chironomid species (last instar larvae < 5 mm).
6. There was considerable fluctuation in the numbers of different species of chironomids from year to year and at Loch Grosvenor, the Tanypodinae did not increase in proportion to the herbivorous chironomid larvae.
7. The increases in biomass are compared with the standing stock of bottom fauna in other lochs. The maximum productive level following fertilization was equivalent to that of a loch with an alkalinity of about 30 mg CaCO_3/l .
8. The two-year delay in the higher production of bottom fauna following the addition of fertilizer may well have been because the fertilizers were taken up by phytoplankton, the mud and macrophytes and only later released to become available to the algae of the mud and the attached algae, which are important foods of the bottom fauna. It is suggested that other kinds of fertilizer, which may produce these latter types of algae more rapidly, should be tested.
9. Measurements of the growth rate of trout up to 1957 are recorded by Munro (1961) from which it appears that the trout did not utilise the increased production of chironomid fauna efficiently. This may have been because the larvae and pupae were only available to trout for a limited period of the year and that the winter feeding in particular was little better than before fertilization. In future experiments it might be profitable to introduce suitable food organisms such as *Gammarus* spp., *Asellus* spp. and *Limnaea peregra* following the application of fertilizer.

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APPENDIX 1

CATCHES OF BOTTOM-LIVING INVERTEBRATES (PER M²) IN LOCHAN AN SMURAICH

	1954	1955	1956	1957	1958	1959	1960	1961
	21 Apr. 19	Oct. 16	Apr. 20	Apr. 11	Sept. 16	Apr. 16	Oct. 8	12 Apr.
Rhabdocoelida	0	0	0	0	0	0	0	0
Oligochaeta	55	9	68	0	56	35	0	95
<i>Leptophlebia vestertina</i> l.	0	0	11	0	0	0	0	0
<i>Sialis lutaria</i> l.	18	27	34	45	0	12	0	24
Trichoptera l.	9	27	0	0	56	106	12	12
Coleoptera l.	0	9	0	11	0	12	0	0
Chironomidae l.	18	36	529	22	101	142	35	83
<i>Ablabesmyia</i> spp. l.	100	209	664	799	676	804	142	154
<i>Procladius</i> spp. l.	27	0	856	11	1341	343	0	130
<i>Orthocladius apicalis</i> Kieff l.	182	0	214	449	360	1148	816	450
<i>Lauterborniella orophilus</i> Edw. l.	64	9	676	281	56	1526	225	450
<i>Tanytarsus</i> spp.	27	55	462	968	191	130	24	154
Other Chironomidae	18	0	11	0	90	35	12	0
Chironomidae p.	9	36	11	23	11	0	0	0
Hydracarina	0	0	45	0	34	0	0	12
Sphaeriidae	527	453	3581	2609	1563	4293	1479	1588
Total Number	788	1362	6337	6974	2502	3891	676	764
Total Weight (mg)	1.5	3.0	1.8	2.7	1.6	0.91	0.46	0.48
Mean wt of organisms (mg)								
				l.—larvae				
				p.—pupae				

APPENDIX 2

CATCHES OF BOTTOM-LIVING INVERTEBRATES (PER M²) IN LOCH GROSVENOR

	1954	1955	1956	1957	1958	1959	1960	1961
	22 Apr. 19	Oct. 20	Apr. 23	Apr. 13	Sept. 19	Apr. 17	Oct. 11	10 Apr.
Oligochaeta	9	9	34	79	293	35	83	154
<i>Helobdella stagnalis</i>	0	0	0	0	0	0	12	0
Ephemeroptera l.	0	0	0	11	11	0	0	0
<i>Sialis lutaria</i> l.	9	36	23	34	34	12	24	0
Trichoptera l.	0	36	56	22	68	83	47	35
Coleoptera l.	0	0	11	0	0	0	0	0
Chironomidae l.	9	36	462	327	113	83	47	0
<i>Ablabesmyia</i> spp. l.	83	182	135	709	383	331	71	95
<i>Procladius</i> spp. l.	18	9	372	180	541	177	47	12
<i>Orthocladius apicalis</i> l.	0	0	56	428	450	378	154	59
<i>Lauterborniella orophilus</i> l.	0	18	338	1689	1791	4434	225	12
<i>Tanytarsus</i> spp. l.	36	354	619	709	496	815	119	35
Other Chironomidae	0	9	11	0	68	35	0	0
Chironomidae p.	0	0	23	0	0	0	0	0
Hemerodromia.	0	18	0	11	0	24	59	12
Hydracarina	0	0	0	0	23	0	0	0
<i>Limnaea peregra</i>	0	0	0	0	518	650	71	0
Sphaeriidae	0	282	23	507	473	7057	994	414
Total Number	163	989	2163	4706	1779	5841	1610	487
Total Weight (mg)	389	1629	3802	9548	1871	5841	866	487
Mean wt of organisms (mg)	2.4	1.6	1.8	2.0	1.1	0.83	0.51	1.2
				l.—larvae				
				p.—pupae				

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